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Citation for published version:

Cox, DTC, Hudson, HL, Plummer, KE, Siriwardena, GM, Anderson, K, Hancock, S, Devine-wright, P, Gaston, KJ & Macivor, JS (ed.) 2018, 'Covariation in urban birds providing cultural services or disservices and people', *Journal of Applied Ecology*, vol. 55, no. 5, pp. 2308-2319.
<https://doi.org/10.1111/jpe.2018.55.issue-5>

Digital Object Identifier (DOI):

[10.1111/jpe.2018.55.issue-5](https://doi.org/10.1111/jpe.2018.55.issue-5)

Link:

[Link to publication record in Edinburgh Research Explorer](#)

Document Version:

Publisher's PDF, also known as Version of record

Published In:

Journal of Applied Ecology

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RESEARCH ARTICLE

Covariation in urban birds providing cultural services or disservices and people

Daniel T. C. Cox¹  | Hannah L. Hudson¹ | Kate E. Plummer^{2,3} | Gavin M. Siriwardena² | Karen Anderson¹ | Steven Hancock⁴ | Patrick Devine-Wright⁵ | Kevin J. Gaston¹ 

¹Environment & Sustainability Institute, University of Exeter, Penryn, UK

²British Trust for Ornithology, The Nunnery, Thetford, UK

³Centre for Ecology & Conservation, College of Life & Environmental Sciences, University of Exeter, Penryn, UK

⁴Global Ecology Lab, Department of Geographical Sciences, University of Maryland, College Park, MD, USA

⁵Geography, Life and Environmental Sciences, University of Exeter, Exeter, UK

Correspondence

Daniel T. C. Cox
Email: d.t.c.cox@exeter.ac.uk

Funding information

Natural Environment Research Council, Grant/Award Number: NE/J015237/1; NERC Biodiversity and Ecosystem Service Sustainability programme, Grant/Award Number: NE/J015237/1

Handling Editor: J. Scott MacIvor

Abstract

1. The spatial distributions of biodiversity and people vary across landscapes and are critical to the delivery of ecosystem services and disservices. The high densities of people and often of birds in urban areas lead to frequent human–avian interactions, which can be positive or negative for people's well-being. The identities of the bird species providing these services or disservices tend to be quite different; however, it is unclear how their abundance and richness covary with human population density, and hence with potential recipients of these services and disservices.
2. We surveyed bird populations in 106 tiles (500 × 500 m) across the 174 km² of an extended urban area in southern England. From the literature, we identified two groups of species: those associated with positive interactions for human well-being and those that display behaviours that are negative for human well-being. We estimated the abundance (adjusted for detection probability) and richness of each group and modelled how they covary with human population density.
3. Aggregation of population estimates for the 35 service and nine disservice species observed revealed 593,128 (95% confidence interval: 541,817–657,046) and 225,491 (200,134–235,066) birds respectively. Across the surveyed tiles, there were 1.09 service and 0.42 disservice birds per person.
4. There was a peaking quadratic relationship between service abundance and human population density, but a negative linear relationship between richness and human density. Conversely, there were positive linear relationships for both abundance and richness of disservice species with human density. The ratio of service to disservice birds shifted from 3.5–1 at intermediate human densities to 1–1 in more densely populated areas.
5. *Synthesis and applications.* Differences in the distributions of service and disservice species, and the extremely low ratios of birds to people particularly in socio-economically deprived areas, mean that people there have few opportunities for contact with birds, and the contact they do have is equally likely to be negative as positive for human well-being. We recommend spatial targeting of improvements in green infrastructure, combined with the targeted provisioning of food and

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nesting places for service species, to promote positive interactions between birds and people.

KEY WORDS

abundance, distribution of species, ecosystem services, human–avian conflict, human–nature interactions, species richness, urban birds, wildlife management

1 | INTRODUCTION

The relationship between the spatial distribution of biodiversity and of people has attracted a good deal of attention (e.g. Gaston, 2005, 2006; Luck, 2007; Sushinsky, Rhodes, Possingham, Gill, & Fuller, 2013; Wilson, Thomas, Fox, Roy, & Kunin, 2004). This has focussed on the oft-reported finding at larger geographic scales of broad-positive relationships between species richness and the number of people in an area, with negative relationships only appearing at high human densities (e.g. Chown, van Rensburg, Gaston, Rodrigues, & van Jaarsveld, 2003; Evans, Greenwood, & Gaston, 2007; Pautasso, 2007; Tratalos et al., 2007). Although more scarce, broadscale-positive spatial relationships between the densities of individuals of particular taxonomic groups and of people have also been documented (e.g. Blair, 2004; Gaston & Evans, 2004; Silva, García, Estay, & Barbosa, 2015; Tratalos et al., 2007). The two patterns have been argued to result from species richness and the densities of other taxa and of people sharing similar responses to spatial variation in environmental variables such as energy availability and habitat diversity (Balmford et al., 2002; Evans & Gaston, 2005; Gaston, 2005; Huston, 2005).

Consideration of the implications of spatial relationships between species richness and numbers of people and between numbers of individuals of other taxa and numbers of people has almost exclusively focussed on conservation issues (e.g. Chown et al., 2003; Pearson, 2016). However, they are also important in terms of the role of biodiversity in the delivery of ecosystem services (benefits provided by ecosystems for human well-being; Millennium Ecosystem Assessment, 2005) and the avoidance of disservices to people (functions of ecosystems that are perceived as negative for human well-being; Lyytimäki & Sipilä, 2009).

Birds can provide an array of ecosystem services such as pollination, pest control and the transport of nutrients (Wenny et al., 2011). Within urban areas, the delivery of cultural services (defined as the non-material benefits people obtain from ecosystems; Millennium Ecosystem Assessment, 2005) may be particularly significant, because of the general paucity of opportunities for positive experiences of nature (Belaire, Westphal, Whelan, & Minor, 2015; Jones, 2011). Indeed, there is substantial evidence that interactions with birds in towns and cities can provide people with feelings of being connected to nature (Cox & Gaston, 2016; Harris, de Crom, & Wilson, 2016) and can have positive effects on human well-being (Belaire et al., 2015; Cox & Gaston, 2016; Cox et al., 2017; Jones, 2011).

Birds are also responsible for some important disservices, including disease transmission and the pollution of water supplies (Araújo et al., 2014). From a cultural services perspective, although individual birds are often thought of positively most of the time (Belaire et al., 2015; Cox & Gaston, 2015; Harris et al., 2016), they can also display behaviours that are considered negative for human well-being, such as aggression, damage to property, depositing faeces and causing unwelcome noise and smells (Charles & Linklater, 2013; Galbreath, Ichinose, Furutani, Yan, & Higuchi, 2014; Rock, 2005). In towns and cities, the proximity of people to these species means that an increased number of people are likely to be exposed to such negative behaviours, and as a consequence, urban areas can be hotspots of human–avian conflict.

The ecological traits of bird species that provide cultural services or disservices tend to be quite different, with service species tending to be aesthetically pleasing and having behaviours that people find interesting to watch (Belaire et al., 2015; Correia, Jepson, Malhado, & Ladle, 2016), while species providing disservices are often omnivorous and larger bodied (Belaire et al., 2015; Charles & Linklater, 2013). Given that both cultural services and disservices tend to be delivered at a local level, this raises a question of the extent to which the abundance or richness of the two bird groups and the numbers of people are spatially correlated, and whether these patterns differ between the groups. Given the existence of the broad-positive relationships between avian abundance or species richness and human density previously mentioned (e.g. Gaston & Evans, 2004), one might predict that species providing cultural services or disservices would similarly respond positively to increased human density. Alternatively, urban areas have the highest densities of people, and thus are also the areas in which overall abundance and richness relationships tend to become negative with increasing human densities as appropriate resources for birds diminish (e.g. Blair, 1996; Silva et al., 2015). This suggests that negative relationships between the abundance and richness of birds providing cultural services or disservices and human densities might prevail.

We carried out extensive bird surveys across an extended urban area in the UK to establish for the first time covariation in populations of birds that provide cultural services or disservices and human population density. From the literature, we identified two groups of species within the surveyed birds: those that are associated with positive interactions for human well-being (cultural services) and those that commonly display behaviours that are negative for human well-being (cultural disservices). We set out to determine the direction

and strength of spatial relationships of the abundance and species richness of both groups and the density of people. Furthermore, the overall levels of services to disservices may be influenced by the whole avian community; therefore, we also test how the ratio of service to disservice birds varied with human population density. We control for socio-economic deprivation of human communities and the quantity of green space, because both have been shown to be associated with bird abundances and richness (e.g. Fuller, Warren, Armsworth, Barbosa, & Gaston, 2008; Silva et al., 2015). Unpacking the spatial relationships between different species, or groups of species, and people in this way is a critical step for informing management recommendations to promote positive interactions between people and birds in urban areas.

2 | MATERIALS AND METHODS

2.1 | Bird abundance and richness

This study was a part of a wider project investigating urban ecosystem services (e.g. see Cox & Gaston, 2016; Cox, Inger, Hancock, Anderson, & Gaston, 2016; Cox et al., 2017; Inger, Cox, Per, Norton, & Gaston, 2016), focused on the urban area of the "Cranfield triangle," a region in southern England, UK (52°07'N, 0°61'W). This comprises the three adjacent towns of Milton Keynes, Luton and Bedford, which have a combined human population of c. 546,000 (Office of National Statistics, 2016) and occupy c. 174 km². They contain great variation in human population density and urban form (including representatives of low- and high-density living). For the wider project, we divided the landscape within the urban limits of the Cranfield triangle into 500 × 500 m square "tiles" (250,000 m²), where tiles within the urban limits were defined as those that had greater than 25% urban built form, as assessed by eye ($n = 695$; Gaston, Warren, Thompson, & Smith, 2005). We used remote-sensing data to calculate two measures of urban form within each tile: percentage tall vegetation cover and percentage building cover (see Appendix S1). We then applied random sampling, stratified to maximize variation in urban form across five categories for each measure, reflecting the range of values found within the urban limits of the Cranfield triangle: tall vegetation cover (0%–10%; >10%–20%; >20%–30%; >30%–40%; >40%) and built cover (0%–5%; >5%–10%; >10%–15%; >15%–20%; >20%; see Table S1). This provided 25 possible urban forms, with up to five tiles then being randomly selected from each form. We conducted extensive bird surveys in the resulting 106 tiles (less than five tiles were available for seven forms; see Table S1). We did this by identifying up to four sampling points in each tile (mean per tile, 3.91 ± 0.32 SD), to represent the diversity of urban forms present as fully as possible. Survey points were selected to be ≥ 200 m apart and ≥ 100 m from tile edges, such that surveys from each point should have sampled different birds for most species. All sampling points were located on public land with easy access for researchers, where such sampling points were unavailable fewer than four points were chosen ($n = 8$).

To measure bird abundance per unit area, we used point counts and a distance sampling procedure to account for differences in detectability among species (Buckland et al., 2001). All point counts were carried out by one of two trained researchers. We conducted two early-morning surveys (06:00–10:00 hours) at each point in all tiles during the breeding season, one in May 2013 and one in June 2013; these were timed to maximize the detectability of the local breeding bird community. Point counts were conducted for 10-min periods, divided into 2-min intervals. Within each 2-min interval, the number of birds and the radial distance from the observer at which they were seen was recorded in bands of 0–20 m, 20–40 m, 40–60 m and 60–100 m. Birds were recorded independently in each 2-min period. Individuals that moved during a 2-min period were recorded in the distance band in which they were first detected. Data are available from the Centre for Ecology and Hydrology. <https://doi.org/10.5285/c4806e25-5325-4b01-8066-91a8fb55eb41> (Plummer & Siriwardena, 2018).

For each individual 10-min point count, we selected the maximum count of each species per distance band from the multiple 2-min intervals. We then combined data from the two visits by selecting the maximum count per band across visits, so providing one maximum overall count per band. We used these data and the `UNMARKED` package (Fiske & Chandler, 2011) to calculate bird abundance corrected for detection probability. To account for the effect of variation in habitat on detection probability at each survey point, we estimated distance-detection functions with respect to percentage vegetation cover >0.7 m tall and percentage built cover within the survey radius. We calculated a pooled detection function for species with similar morphology and behaviour, assuming that these species had similar detection characteristics (see Table S2). This is because a number of species had sample sizes of less than 40 individuals, which precluded appropriate distance analysis on these individual species (see Table S2). For each survey point, we then calculated an adjusted measure of abundance and associated 95% confidence intervals by dividing raw abundance counts for each species by its detection probability. We then summed the adjusted abundances from the survey points within each tile, before scaling these up to the area of the tile by multiplying these summed adjusted abundances by the total area of the tile (250,000 m²) divided by the total area surveyed within the tile (depending on whether three or four points had been surveyed).

2.2 | Species providing cultural ecosystem services and disservices

Based on the literature, we identified two distinct groups of birds within the surveyed bird community, one group providing cultural services and a second group providing cultural disservices.

2.2.1 | Cultural service providers

Songbirds and woodpeckers cohabit with people in residential neighbourhoods and are usually thought of positively (Belaire

et al., 2015; Brock, Perino, & Sugden, 2017; Clergeau, Mennechez, Sauvage, & Lemoine, 2001; Clucas, Rabotyagov, & Marzluff, 2015; Vuorisalo, Lahtinen, & Laaksonen, 2001). Indeed, watching birds in the garden has been associated with increased feelings of relaxation and connectedness to nature (Cox & Gaston, 2016), while feeding garden birds provides people with a sense of pleasure (e.g. Galbraith et al., 2014; Jones, 2011). Listening to birdsong can increase people's appreciation of landscapes (Hedblom, Heyman, Antonsson, & Gunnarsson, 2014), by contributing towards mental restoration and stress relief (Ratcliffe, Gatersleben, & Sowden, 2013). Interacting with songbirds and woodpeckers around the home is easily accessible to most people, with the economic value of enjoying common native urban songbirds in Berlin, Germany, having been estimated to be 70 million USD/year (Clucas et al., 2015). We, therefore, consider that songbirds and woodpeckers are a distinct group for the provision of cultural services (Table 1).

2.2.2 | Cultural disservice providers

Human-avian conflict often arises due to the behaviours of a small number of species, which are perceived to be negative by people (Charles & Linklater, 2013). These behaviours, among others, include aggression towards humans (e.g. Canada goose *Branta canadensis*; Smith, Craven, & Curtis, 2000, and individuals being noisy, destructive or causing mess through their faeces or foraging behaviours (e.g. Herring gull *Larus argentatus*; Clergeau et al., 2001; Rock, 2005). For each surveyed species, we used extensive literature searches for evidence of commonly occurring human-avian conflict in urban areas (Web of Science, Google Scholar and Google; keywords utilized included "species name," "conflict," "wildlife management"). We only included studies conducted in Northern Europe, where urban areas have similar avian communities to the study site. All species have been identified by Natural England as pest species that can be taken or killed under "Wild birds: general licence to take or kill for health and safety purposes" (Table 1, see Table S3).

2.2.3 | Scaling up abundances of cultural service and disservice birds to the urban landscape

For each surveyed tile, we calculated the summed adjusted abundance, along with associated 95% confidence intervals, for species providing cultural services and disservices (see Table S1). To scale up estimates to the urban landscape, we averaged the adjusted abundance of each group for surveyed tiles from each urban form (based on the vegetation and building cover; see Table S1). We then applied these averaged abundances for each group to the total number of surveyed and non-surveyed tiles that had equivalent urban forms and fell within the urban limits of the Cranfield triangle (see Table S1). Finally, we summed adjusted abundances across all tiles to estimate the total abundance of those species providing cultural services and those providing cultural disservices (see Table S1). In each surveyed tile, we also calculated species richness for each group (see Table S1).

2.2.4 | Human population density, socio-deprivation and green space

For each survey tile, we estimated the human population density based on the UK-gridded population map (Reis et al., 2016). This dataset is based on the 2011 Census data (Office of National Statistics, 2016) and Centre for Ecology and Hydrology Land Cover Map 2007 and consists of gridded population data with a spatial resolution of 1 km², assigned to the UK National Grid. For each surveyed tile, we scaled the estimated human population relative to the area of the gridded population square that the tile covered (i.e. up to 25%). Where the survey tile covered more than one population square, we weighted our estimate by the proportion of that tile that was covered.

Socio-economic deprivation of human communities has been shown to be negatively correlated with bird abundance and richness (Fuller et al., 2008). To arrive at a generalized measure of deprivation for each tile, we used weekly household wages. These were derived from model-based estimates for households (Office of National Statistics; <http://www.neighbourhood.statistics.gov.uk/HTMLDocs/incomeestimates.html>). This index estimates income per household per week in pounds sterling, from data identified during the period from April 2007 to April 2008. The household data were averaged across the Middle Layer Super Output Area (MSOA), a geographical hierarchy consisting of 2,000–6,000 households and were the most recent data currently available. We scaled the income relative to the MSOA covered by the tile, where a tile covered multiple MSOAs we weighted by the percentage of tile each MSOA covered.

Avifaunal diversity is strongly associated with green space structure, diversity and complexity in urban areas (e.g. Evans et al., 2007; Sandström, Angelstam, & Mikusiński, 2006). Therefore, because urban green space consists of large areas of grass as well as shrubs and trees, we used airborne hyperspectral data at 2 m resolution to calculate the proportion of green space in each surveyed tile (instead of vegetation exceeding 0.7 m in height as used to estimate urban form; see Appendix S1). Green space was defined as the percentage of pixels in the tile at 2 m resolution that had a Normalized Difference Vegetation Index (NDVI; a well-established indicator of whether a pixel contains photosynthesising material or not) exceeding a threshold of 0.2 (i.e. that were vegetated, see Appendix S1).

2.3 | Statistical analysis

We created two response variables for each of cultural service and disservice birds: abundance and richness per tile. All four resulting response variables were approximately normally distributed. We then built linear mixed models of human population density, weekly household income and green space against each response variable in turn. As population densities often form nonlinear relationships, we repeated each model twice, instead fitting first a quadratic and then a higher order polynomial function to human population density. Of these three models, we selected the one with the lowest AIC, before using the MuMIn package (Bartoń, 2015) to produce

Species	Occupancy (%)	M (SE)	Range
Cultural service providers			
Green woodpecker <i>Picus viridis</i>	25	3 (1)	0–8
Great-spotted woodpecker <i>Dendrocopos major</i>	25	3 (2)	0–7
Skylark <i>Alauda arvensis</i>	10	1 (1)	0–3
Pied wagtail <i>Motacilla alba</i>	21	5 (4)	0–16
Dunnock <i>Prunella modularis</i>	100	8 (5)	0–25
Robin <i>Erithacus rubecula</i>	100	10 (5)	1–32
Blackbird <i>Turdus merula</i>	100	15 (9)	2–108
Song thrush <i>T. philomelos</i>	68	5 (4)	0–30
Mistle thrush <i>T. viscivorus</i>	9	6 (4)	0–18
Garden warbler <i>Sylvia borin</i>	21	4 (2)	0–10
Blackcap <i>S. atricapilla</i>	73	6 (3)	0–21
Whitethroat <i>S. communis</i>	29	7 (3)	0–16
Lesser whitethroat <i>S. curruca</i>	5	5 (3)	0–10
Sedge warbler <i>Acrocephalus schoenobaenus</i>	5	5 (3)	0–10
Reed warbler <i>A. scirpaceus</i>	8	6 (3)	0–16
Chiffchaff <i>Phylloscopus collybita</i>	40	3 (1)	0–7
Willow warbler <i>P. trochilus</i>	8	4 (2)	0–7
Wren <i>Troglodytes troglodytes</i>	91	7 (4)	0–22
Great tit <i>Parus major</i>	89	8 (4)	0–36
Coal tit <i>Periparus ater</i>	16	10 (8)	0–34
Blue tit <i>Cyanistes caeruleus</i>	100	15 (8)	1–45
Marsh tit <i>Poecile palustris</i>	1	–	12
Long-tailed tit <i>Aegithalos caudatus</i>	31	15 (9)	0–40
Goldcrest <i>Regulus regulus</i>	13	9 (4)	0–23
Nuthatch <i>Sitta europaea</i>	2	11 (5)	0–18
Treecreeper <i>Certhia familiaris</i>	5	8 (3)	0–12
Starling <i>Sturnus vulgaris</i>	93	24 (35)	0–320
House Sparrow <i>Passer domesticus</i>	89	29 (21)	0–139
Chaffinch <i>Fringilla coelebs</i>	100	8 (5)	0–38
Linnet <i>Carduelis cannabina</i>	9	7 (3)	0–14
Goldfinch <i>C. carduelis</i>	100	11 (8)	0–49
Greenfinch <i>C. chloris</i>	96	8 (5)	0–27
Bullfinch <i>Pyrrhula pyrrhula</i>	15	13 (7)	0–32
Yellowhammer <i>Emberiza citrinella</i>	2	5 (3)	0–7
Reed bunting <i>E. schoeniclus</i>	10	4 (1)	0–7
Cultural disservice providers			
Black-headed gull <i>Chroicocephalus ridibundus</i>	8	4 (1)	0–5
Herring gull <i>Larus argentatus</i>	12	7 (8)	0–32
Lesser black-backed gull <i>L. fuscus</i>	42	11 (8)	0–35
Feral pigeon <i>Columba livia</i>	64	19 (38)	0–356
Stock dove <i>C. oenas</i>	10	3 (1)	0–6
Wood pigeon <i>C. palumbus</i>	100	17 (11)	3–98
Magpie <i>Pica pica</i>	99	8 (6)	0–41
Carrion crow <i>Corvus corone</i>	100	8 (6)	3–50
Jackdaw <i>C. monedula</i>	72	9 (9)	0–44

TABLE 1 The distribution and raw abundance, of survey points in each 500 × 500 m tile, of species providing cultural services and disservices. We show the percentage of occupied tiles that were surveyed, the mean number of birds recorded at survey points per occupied tile and the range of counts recorded

all subsets of models based on that global model and ranking them based on ΔAIC_c . Following Richards (2005), we retained all models where $\Delta AIC_c < 6$. We then used model averaging to produce the coefficients with standard errors and 95% confidence intervals, of each retained parameter (Burnham & Anderson, 2002).

To explore how the ratio of birds providing services to those providing disservices varied with human population density, we created two response variables, the ratio of the abundance of cultural service to disservice providers and the ratio of the richness of cultural service to disservice providers. We logged both response variables approximately to normalize the distribution of the data and again applied a quadratic function to human population density. We then built a linear model for each response variable and averaged models as above.

3 | RESULTS

Across the 106 tiles (total area of 26.5 km²), we estimated 91,577 (95% confidence interval [CI]: 83,545–101,592) individual birds of 35

species that provide cultural services, and 34,299 (32,019–37,645) individual birds of nine species that provide cultural disservices (Table 1 for summary by species; see Table S1 for summary by tile; Figure 1). These two groups captured 91% of individuals and 61% of all species recorded. Scaled up across the urban landscapes we estimated, there were 593,128 (541,173–657,046) individual cultural service birds and 225,491 (210,674–247,438) cultural disservice birds.

3.1 | Abundance and richness and human population density

Quadratic regression outperformed higher order polynomial and linear regression in describing the relationship between cultural service bird abundance and human population density, with abundance peaking at c. 1,100 people per 500 × 500 m (Table 2; Figure 2a). The abundance also increased with the percentage green space (Table 2). The species richness of cultural service birds decreased with human population density but increased with percentage green space (Table 2). There was a positive linear relationship between the

FIGURE 1 Frequency distributions across survey tiles of the abundance and richness of two sets of avian species, one that provides cultural services (a & b respectively) and one that provides cultural disservices (c & d respectively)

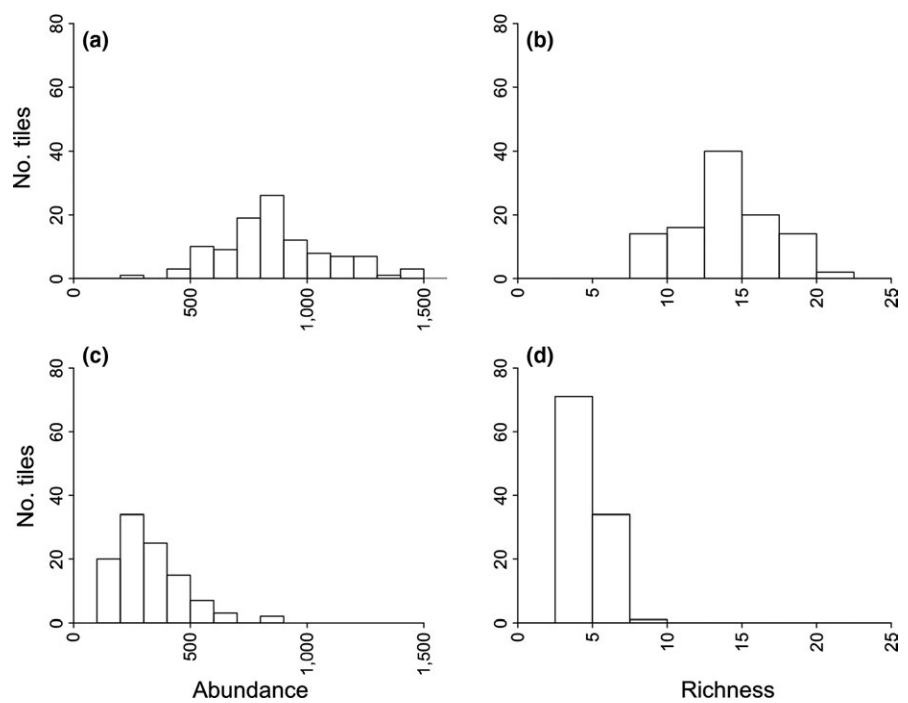


TABLE 2 The direction and shape of spatial relationships of the abundance and richness of groups of birds providing cultural services and disservices with human population density. We controlled for the estimated household weekly income and the quantity of green space. We show model averaged parameter estimates and standard errors, adjusted R^2 are from global models

Response	Variable	Intercept	Population	Population ²	Income	Green space	R^2
Service	Abundance	498 (135)***	0.51 (0.14)***	-2.2e-4 (6.3e-5)***	-1.8e-4 (1.5e-2)	379 (137)**	.20
	Richness	11.3 (1.6)***	-2.0e-3 (1.0e-3)***		1.8e-3 (1.7e-3)	6.5 (1.6)***	.28
Disservice	Abundance	205 (79)*	0.13 (0.03)***		-0.09 (0.09)	153 (79)*	.24
	Richness	8.1e-1 (3.1e-1)*	8.13e-4 (2.5e-4)**		-1.1e-3 (7.4e-4)	1.0 (0.7)	.16

Statistical significance: * $p < .05$; ** $p < .01$; *** $p < .001$.

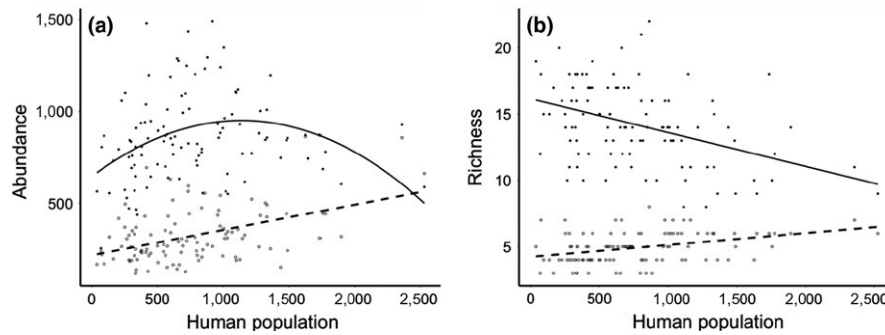


FIGURE 2 Human population density (500×500 m) and (a) abundance and (b) richness of sets of avian cultural service (solid line and circles) and cultural disservice (dashed line and hollow circles) providers. Quadratic regression outperformed higher order polynomial regression in describing the relationship between service bird abundance and predictors. Linear regression outperformed quadratic and higher order polynomial regression in describing service richness and disservice abundance and richness with predictors. In each case, we show the model fit as the line of best fit

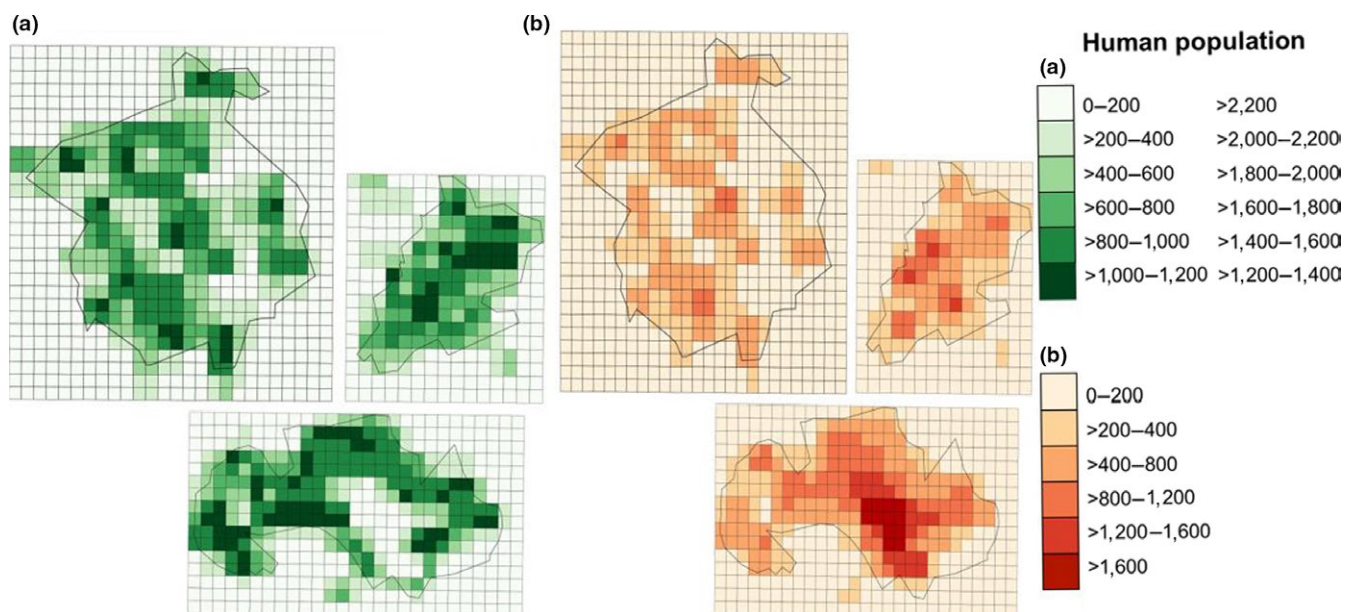


FIGURE 3 Spatial variation in the provision of (a) services and (b) disservices by urban birds. Colour gradient bands show the predicted abundance of (a) service (quadratic) and (b) disservice (linear) bird populations, estimated based on the covariation in each group with human population density (Figure 2). Service or disservice provision will be greatest with increased bird abundances, with service birds showing a quadratic relationship with human population density, and disservice birds a linear one. The lightest colour indicates least abundance, and the darkest colour shows greatest abundance of service or disservice birds. Due to the necessary difference in scales, it is not possible to directly compare services with disservices; however, the figure provides an interesting indication of how the two are spatially distributed. The black line shows the urban limits of Milton Keynes (top left), Bedford (top right) and Luton (bottom), in each figure [Colour figure can be viewed at wileyonlinelibrary.com]

abundance and richness of cultural disservice species and human population density and the availability of green space (Table 2; Figure 2b).

Based on the parameter estimates from the models, we mapped how the abundance of service and disservice birds covaried with human population density. Scaled up across the landscape, service and disservice birds showed distinctly different spatial patterns. Service birds were most abundant in areas of medium housing density, in the suburbs (Figure 3a), while disservice birds were most abundant in areas of dense housing, such as those around urban centres (Figure 3b).

3.2 | The ratio of cultural service to disservice birds with human population density

The abundance and richness of cultural service and disservice providers were only weakly correlated (Pearson's correlation coefficient = 0.07 and 0.40 respectively). Across the urban landscape, there were equivalent to 1.09 cultural service and 0.42 cultural disservice birds for every human. Quadratic regression outperformed higher order polynomial and linear regression in describing the relationship between the ratio of cultural service to disservice providers and human population density, with c. 3.5 cultural service

TABLE 3 The direction and shape of the spatial relationships between the ratios of abundance and richness of birds providing cultural services to those providing cultural disservices with human population density. We show model-averaged parameter estimates and standard errors (in parentheses). Adjusted R^2 are from global models

Response	Intercept	Population	Population ²	Income	Green space	R^2
Ratio abundance	1.0 (0.2)***	5.8e-4 (2.6e-4)*	-4.0e-7 (1.2e-7)**	2.0e-3 (2.9e-4)	-5.4e-2 (2.6e-1)	.16
Ratio richness	9.0e-1 (2.0e-1)***	-3.3e-4 (6.5e-5)***	-	3.8e-4 (1.8e-4)*	3.0e-4 (1.8e-4)*	.38

* $p < .05$; ** $p < .01$; *** $p < .001$.

birds to each cultural disservice bird at human population densities of 1,000 people per 500 × 500 m (estimated peak cultural service provision). Linear regression best described the negative relationship between the ratio of cultural service to disservice birds and increasing human population density (Table 3; Figure 4). We also found that weekly household income was positively correlated with an increased ratio of cultural service to disservice species (Table 3).

4 | DISCUSSION

Avian abundance and richness changed markedly with spatial variation in human population density, with those birds that provided cultural services showing distinctly different spatial relationships from those providing cultural disservices (Figure 3). Presumably, these relationships are not a direct consequence of human population density per se, but instead occur indirectly as a result of factors such as urban form (Silva et al., 2015; Tratalos et al., 2007), private and public green space management (Sandström et al., 2006), disturbance (Matlack, 1993) and resource availability (e.g. Gaston et al., 2007), all of which vary along socio-economic gradients (Davies, Fuller, Dallimer, Loram, & Gaston, 2012).

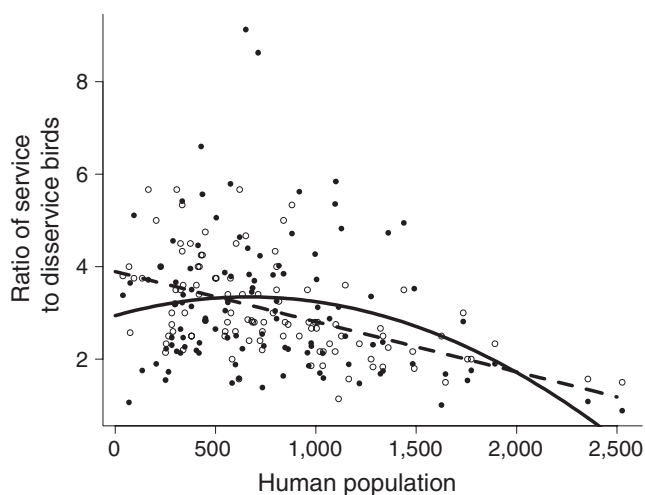


FIGURE 4 The relationship between the ratio of abundance (solid line and circles) and richness (dashed line and hollow circles) of cultural service to disservice providers and human population density (500 × 500 m). Quadratic regression outperformed higher order polynomial regression in describing the relationship between the ratio of service to disservice bird abundance and predictors, and the result of this model is shown as the best fit line

Scaled up across the urban landscape, we show that there were over two and a half times as many birds and species that were positive for people's well-being than those whose behaviours commonly cause conflict. This leads to 1.09 cultural service birds and 0.42 cultural disservice birds for every person. Allowing that 91% of surveyed individuals were captured by these two groups, this is higher than the total of 1.18 birds per person reported by Fuller, Tratalos, and Gaston (2009) in a UK city with a population of approximately the same size as that of the Cranfield triangle. This is perhaps unsurprising considering that approximately half of the urban study area consists of a planned green town, and therefore, contains large levels of green space. It also illustrates the large variation that can occur in avian abundances between urban areas of similar human populations and latitudes, but with different topographies, green space distributions, histories and forms.

Spatially, the abundance of birds providing cultural services was greatest in tiles of medium human population density (Figure 3a), with these areas usually consisting of a diverse mosaic of private and public green spaces, often with well-tended, hyper-diverse biota (Goddard, Dougill, & Benton, 2010). This suggests that people living in these areas are likely to encounter cultural service birds more frequently and so gain positive psychological experiences (Cox et al., 2017). This is consistent with previous studies in the UK that have documented relationships for some bird species that are considered indicators of urban biodiversity (Tratalos et al., 2007; indicator T3: DEFRA, 2002; indicator T1: DEFRA, 2003). There was a significant variation in abundance and richness of cultural service birds among tiles of urban forms with similar levels of vegetation and building cover, indicating that the flow of cultural services responds to factors other than those measured here, such as the presence of roads (Cox et al., 2016) and the provision of resources by people (Fuller et al., 2008; Galbraith, Beggs, Jones, & Stanley, 2015).

Spatially, there was a positive relationship between the abundance of cultural disservice birds and human population density, with abundances being highest in areas of dense housing and in urban centres (Figure 3b). Abundances were independent of green space availability, suggesting that these species tend to be urban exploiters. High densities of birds and people within the same geographical area increase the probability that a human-avian interaction will occur. At these increased densities, if a bird displays behaviours that people perceive as negative, such as acts of aggression towards humans, destruction of property or the defacing of buildings and cars with faeces, then the increased frequency of these interactions might exceed cultural tolerance and result in conflict (Decker & Purdy, 1988). Indeed, the level of a problem, such as noise or the quantity of faeces, is likely to be proportional to both

the number of birds in the population and the number of people that could potentially experience the negative behaviour. Reductions in the rates of interactions, driven by the management to reduce carrying capacity or opportunities for people to encounter problem species, would therefore reduce disservices. Action plans to mitigate conflict should consider targeted management of individuals and populations of birds in problem areas in this context, rather than extirpation programmes that are likely not to be feasible logistically.

The relationships between the richness of cultural service and disservice species with human population density were distinctly different, with cultural service species richness decreasing and disservice richness increasing. The cultural service species examined here (songbirds and woodpeckers) are known to respond to habitat availability (e.g. Melles, Glenn, & Martin, 2003), and we found that green space was a strong predictor of their richness and abundance. Despite the negative relationship between cultural service richness and human population density, cultural service species abundance showed a quadratic relationship, peaking at medium human population densities, suggesting an increase in abundance of a small number of species. This supports previous work that found that garden bird feeding, which tends to be prevalent in areas of medium housing density (Davies et al., 2012), supports an increased abundance of feeder-using birds, but not richness (Fuller et al., 2008). The richness and abundance of cultural disservice birds increased with human population density, suggesting that these species have a high tolerance to anthropogenic disturbance. Furthermore, increased richness of these species broadens the range of negative behaviours, so increasing the diversity of cultural disservices as the number of people who can experience these behaviours also increases.

Reflecting the patterns described above, the ratio of cultural service to disservice providers varied with human population density (Figure 4). This has important implications not only for human-avian interactions but also for perceptions of these interactions (Savard, Clergeau, & Mennechez, 2000), which will influence the associated well-being outcomes (Shanahan et al., 2015). The decrease in the ratio of cultural service to disservice providers from 3.5:1 to 1:1 suggests that, at higher human population densities (>2,000 people per 500 × 500 m), all else being equal, there is a 50% chance that a human-avian interaction is with a species that may be perceived negatively. We found that the ratio of service to disservice species decreased with income, suggesting that communities who are already socially deprived are exposed to more species with negative behaviours than wealthier communities, but without the positive influence of service birds. An increased frequency of negative interactions may cause a negative shift in human population perceptions of birds in these areas, which has implications for shaping people's connections to nature and broader support for the conservation of the natural world (reviewed by Restall & Conrad, 2015). Further research is required to investigate spatial variation in perceptions of birds across varying socio-demographic contexts and urban forms and changing ratios of abundance of service to disservice species.

The low ratios of birds to people in some areas within the Cranfield triangle suggest that many people have few opportunities

for contact with birds around their homes, and the contact that they do have may be equally likely to be a negative as positive for human well-being. Positive interactions between birds and people are further inhibited by lower levels of green space in these areas, which often contain poorer quality habitat for birds and people than in more affluent neighbourhoods. These two factors are likely to be important contributors towards people's lack of engagement with birds in these areas, as seen through the reduced occurrence of activities such as bird feeding (e.g. Davies et al., 2012).

4.1 | Management recommendations

Understanding the patterns of cultural service and disservice provision by birds is an important step towards making recommendations for best management practices that support positive interactions between birds and people. Practices might involve both municipal policies and individual actions by householders. First, we recommend that local government bodies invest in green space habitat quality for birds (e.g. by increasing vegetation cover and complexity) in areas with socially deprived human populations, thus increasing the flow of birds that are positive for human well-being into these areas (e.g. Cox et al., 2016). Second, management plans for public green space should act to mitigate conflict with individuals of problem species before it begins, such as through the removal of potential nesting places or food sources to reduce carrying capacity for such species. To our knowledge, policies of this kind have yet to be introduced in Europe.

At the householder level, numerous opportunities exist for attracting birds to gardens, through practices such as wildlife gardening, which are widely promoted by conservation charities and garden retailers. However, the potential of these activities to increase not only the positive interactions with birds for individual households but also the likelihood of neighbouring households having such interactions is not widely recognized. A small number of people thus have the potential positively to impact on health benefits for the wider population from interacting with birds and this could support new campaigns to promote wildlife-friendly gardening, perhaps combined with encouragement to engage in citizen science. Finally, the impact on urban bird populations of the promotion of positive interactions with garden birds by conservation organizations is unclear, practices such as garden bird feeding are likely to have significant population effects (e.g. Plummer, Siriwardena, Conway, Risely, & Toms, 2015), offering a further incentive for households to manage for wildlife.

All management measures should be tailored, using ecological knowledge, to increase the ratio of service to disservice providers, so increasing the relative frequency of positive interactions with birds, the associated well-being benefits people receive and, through positive feedback loops, their desire to seek these benefits.

ACKNOWLEDGEMENTS

We thank M. Evans and M. Gregory for their fieldwork, and J. Harris and R. Corstanje for their advice and logistical support. All authors were supported by the Fragments, Functions, Flows and Urban

Ecosystem Services project, NERC grant NE/J015237/1, funded under the NERC Biodiversity and Ecosystem Service Sustainability programme. The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

D.T.C.C. and K.J.G. conceived and designed the study. K.E.P. and G.M.S. designed and implemented the bird surveys. K.A. and S.H. produced the remote sensing layers. D.T.C.C., H.L.H. and K.J.G. wrote the paper. All authors contributed critically to the drafts and gave final approval for publication of the paper. This research has not been previously presented elsewhere.

DATA ACCESSIBILITY

Airborne lidar and optical data from the four NERC-ARSF flights are available from the Centre for Environmental Data Analysis (CEDA) portal. Users will need to complete a short online registration in order to create a free CEDA account and access the data. DOI: <https://doi.org/10.5285/66513a25354543be9ea7587344cbb87a>; DOI: <https://doi.org/10.5285/5732da3b616843b19db7ff69598abf2c>; DOI: <https://doi.org/10.5285/c1bd61f95443402d8b34a91eeea903e5>; DOI: <https://doi.org/10.5285/24c097cf77474644a4b3b17286abcd91> (NERC Airborne Research and Survey Facility, 2018a,b,c,d).

The bird survey data is under embargo until 31 December 2018, after which it will be available from the Centre for Ecology and Hydrology. <https://doi.org/10.5285/c4806e25-5325-4b01-8066-91a8fb55eb41> (Plummer & Siriwardena, 2018).

ORCID

Daniel T. C. Cox  <http://orcid.org/0000-0002-3856-3998>

Kevin J. Gaston  <http://orcid.org/0000-0002-7235-7928>

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SUPPORTING INFORMATION

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How to cite this article: Cox DTC, Hudson HL, Plummer KE, et al. Covariation in urban birds providing cultural services or disservices and people. *J Appl Ecol*. 2018;55:2308–2319. <https://doi.org/10.1111/1365-2664.13146>